# Biodiversity–multifunctionality relationships depend on identity and number of measured functions

Meyer, Sebastian T ; Ptacnik, Robert ; Hillebrand, Helmut ; Bessler, Holger ; Buchmann, Nina ; Ebeling, Anne ; Eisenhauer, Nico ; Engels, Christof ; Fischer, Markus ; Halle, Stefan ; Klein, Alexandra-Maria ; Oelmann, Yvonne ; Roscher, Christiane ; Rottstock, Tanja ; Scherber, Christoph ; Scheu, Stefan ; Schmid, Bernhard ; Schulze, Ernst-Detlef ; Temperton, Vicky M ; Tscharntke, Teja ; Voigt, Winfried ; Weigelt, Alexandra ; Wilcke, Wolfgang ; Weisser, Wolfgang W

Abstract: Biodiversity ensures ecosystem functioning and provisioning of ecosystem services, but it remains unclear how biodiversity–ecosystem multifunctionality relationships depend on the identity and number of functions considered. Here, we demonstrate that ecosystem multifunctionality, based on 82 indicator variables of ecosystem functions in a grassland biodiversity experiment, increases strongly with increasing biodiversity. Analysing subsets of functions showed that the effects of biodiversity on multifunctionality were stronger when more functions were included and that the strength of the biodiversity effects depended on the identity of the functions included. Limits to multifunctionality arose from negative correlations among functions and functions that were not correlated with biodiversity. Our findings underline that the management of ecosystems for the protection of biodiversity cannot be replaced by managing for particular ecosystem functions or services and emphasize the need for specific management to protect biodiversity. More plant species from the experimental pool of 60 species contributed to functioning when more functions were considered. An individual contribution to multifunctionality could be demonstrated for only a fraction of the species.

DOI: https://doi.org/10.1038/s41559-017-0391-4

# Biodiversity–multifunctionality relationships depend on identity and number of measured functions

Sebastian T. Meyer*[1], Robert Ptacnik[2], Helmut Hillebrand[3], Holger Bessler[4], Nina Buchmann[5], Anne Ebeling[6], Nico Eisenhauer[7,8], Christof Engels[4], Markus Fischer[9], Stefan Halle[6], Alexandra-Maria Klein[10], Yvonne Oelmann[11], Christiane Roscher[12,7], Tanja Rottstock[13], Christoph Scherber[14], Stefan Scheu[15], Bernhard Schmid[16], Ernst-Detlef Schulze[17], Vicky M. Temperton[17,18], Teja Tscharntke[19], Winfried Voigt[6], Alexandra Weigelt[7,8], Wolfgang Wilcke[20], Wolfgang W. Weisser[1]

[1]Terrestrial Ecology Research Group, Department of Ecology and Ecosystem Management, School of Life Sciences Weihenstephan, Technical University of Munich, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany

[2]WasserCluster Lunz, Dr. Carl Kupelwieser Promenade 5, 3293 Lunz am See, Austria

[3]Institute for Chemistry and Biology of Marine Environments [ICBM], Carl-von-Ossietzky University Oldenburg, Schleusenstrasse 1, 26382 Wilhelmshaven, Germany

[4]Humboldt-Universitaet zu Berlin, Institute of Plant Nutrition, Albrecht-Thaer-Weg 4, 14195 Berlin, Germany

[5]Institute of Agricultural Sciences, ETH Zurich, Universitätsstrasse 2, 8092, Zurich, Switzerland

[6]Institute of Ecology, University of Jena, Dornburger Str. 159, D–07743 Jena, Germany

[7]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany

[8]Institute of Biology, Leipzig University, Johannisallee 21, 04103 Leipzig, Germany

[9]Institute of Plant Sciences, University of Bern, Altenbergrain 21, Bern, CH-3013, Switzerland

[10]Chair of Nature Conservation & Landscape Ecology, University of Freiburg, Tennenbacher Str. 4, 79106 Freiburg, Germany

[11]Geoecology, University of Tübingen, Rümelinstraße 19-23, 72070 Tübingen, Germany

[12]UFZ, Helmholtz Centre for Environmental Research, Physiological Diversity, Permoserstrasse 15, 04318 Leipzig, Germany

[13]Institute of Biochemistry and Biology, Biodiversity Research/Systematic Botany, University of Potsdam, Maulbeerallee 1, 14469 Potsdam, Germany

[14]Institute of Landscape Ecology, University of Muenster, Heisenbergstr. 2, 48149 Muenster, Germany

[15]J.F. Blumenbach Institute of Zoology and Anthropology, University of Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany

[16]Department of Evolutionary Biology and Environmental Studies & Zurich-Basel Plant Science Center, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland

[17]Max Planck Institute for Biogeochemistry, Hans-Knoell-Strasse 10, 07745 Jena, Germany

[18]Institute of Ecology, Leuphana University Lüneburg, Scharnhorststrasse 1, 21335 Lüneburg, Germany

[19]Agroecology, University of Göttingen, Grisebachstrasse 6, 37077 Göttingen, Germany

[20]Institute of Geography and Geoecology, Karlsruhe Institute of Technology (KIT), Reinhard-Baumeister-Platz 1, 76131 Karlsruhe, Germany

*Dr. Sebastian T. Meyer, Technical University of Munich, Department of Ecology and Ecosystem Management, Terrestrial Ecology Research Group, School of Life Sciences Weihenstephan, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany, Tel. +49 8161 71 4219, Email sebastian.t.meyer@tum.de

**Biodiversity ensures ecosystem functioning and provisioning of ecosystem services, but it remains unclear how biodiversity–ecosystem multifunctionality relationships depend on the identity and number of functions considered. Here we demonstrate that ecosystem multifunctionality, based on 82 indicator variables of ecosystem functions in a grassland biodiversity experiment, increased strongly with increasing biodiversity. Analysing subsets of functions showed that effects of biodiversity on multifunctionality were stronger when more functions were included and that the strength of the biodiversity effects depended on the identity of the functions included. Limits to multifunctionality arose from negative correlations among functions and functions which were not correlated with biodiversity. Our findings underline that managing of ecosystems for the protection of biodiversity cannot be replaced by managing for particular ecosystem functions or services and emphasise the need for specific management to protect biodiversity. More species from the experimental plant species pool of 60 species contributed to functioning when more functions were considered. An individual contribution to multifunctionality could be demonstrated for only a fraction of the species.**

Ecosystem services, such as the supply of clean water, soil erosion control, or pollination, depend on ecosystem functions that are controlled by the species living in an ecosystem[1]. Provisioning of these services is thought to be threatened by an ongoing loss of species worldwide[2], driven largely by land-use change and overexploitation of natural populations[3]. Ecosystem functioning has been shown to decrease with decreasing biodiversity in experiments that manipulate plant species richness[4]. However, when individual functions are considered, species richness-ecosystem function relationships frequently saturate at low levels of species richness, e.g. when three to six species are present in the system[5,6]. Such saturating relationships have been taken as support for the redundancy hypothesis[7-9], which proposes

77 that high functioning can be achieved with only a few species. However, redundant species
78 may contribute to maintaining ecosystem functions when other species are lost, or under
79 changing environmental conditions[10], referred to as the insurance effect[10,11]. Also, a turnover
80 in the identity of species contributing to a particular function may increase the cumulative
81 number of species sustaining functioning over multiple years[12]. However, even with such
82 mechanisms accounted for, a large part of species still seem to be redundant[13]. This limit to
83 the number of species needed for ecosystem functioning has raised questions if provisioning
84 of ecosystem services can be a major argument for species conservation[14].
85
86 Humans rely on ecosystems for their ability to maintain multiple functions and services
87 simultaneously, as expressed in the concept of ecosystem multifunctionality[15,16]. The number
88 of species contributing to ecosystem multifunctionality is in general higher than the number of
89 species needed for single functions[17-22], and also rare species have been shown to contribute to
90 multifunctionality[23]. Thus, the importance of biodiversity for multifunctionality is higher than
91 for individual functions. When multiple years, places, and environmental change scenarios
92 (so-called contexts) were considered simultaneously by synthesising 12 functions across 17
93 biodiversity experiments, 84%, yet not all, of the 147 grassland plant species studied,
94 promoted ecosystem functioning in at least one context[20]. In addition to the question of
95 whether all species are needed to maintain ecosystem multifunctionality, an equally important
96 question is if and how the effect of biodiversity on ecosystem multifunctionality depends on
97 the identity and number of functions considered[24]. While a recent simulation study found no
98 relationship between the number functions included and the relationship between biodiversity
99 and ecosystem multifunctionality[24], this question remains untested with empirical data. This
100 question is important as different ecosystem functions not only differ in how strongly they
101 depend on biodiversity[25], but biodiversity and ecosystem functions may also be positively or
102 negatively correlated with each other. If ecosystem functions are positively correlated and

depend on biodiversity, then increasing biodiversity can increase many functions simultaneously. In this case, maximising ecosystem multifunctionality will require high biodiversity. Consequently, maximising multifunctionality would be equivalent to maximising biodiversity. However, if functions are negatively correlated, then maximising one function will result in decreasing the other function, and the relationship between ecosystem multifunctionality and biodiversity will depend on the particular functions considered and how they are correlated with biodiversity. The same holds true if functions are uncorrelated, in which case they can be independently maximised. Thus, for the question whether managing for ecosystem multifunctionality is equivalent to managing for a protection of biodiversity, both the relationships among the different functions considered, and the dependence on biodiversity are important.

Here, we analysed the correlation structure of a suite of ecosystem functions to test the hypothesis that strong effects of biodiversity on ecosystem multifunctionality depend on a large and diverse portfolio of functions to be included in the analysis that reflects the high complexity of ecosystem functioning in nature. We base our analyses on a selection of 82 different ecosystem variables identified from a larger collection[25] that were measured along a gradient of 1–60 plant species in a single biodiversity experiment (the Jena Experiment[26], methods). Consistent with previous studies on ecosystem multifunctionality, we approximate ecosystem functions by ecosystem variables[19,20,22,27]. These variables quantify ecosystem functions either directly ("the changes in energy and matter over time and space through biological activity" sensu Reiss, et al. [28]) or indirectly ("key ecosystem properties affected by ecosystem functions" sensu Jax [29]). Restricting analyses of multifunctionality to only directly measured functions would bias the portfolio of included functions considerably, because some types of functions, especially species interactions and belowground functions, are notoriously difficult to measure directly. The best way to include these functions into an analysis of

129 multifunctionality is quantifying state changes or differences in the size of ecosystem
130 compartments as indicators for the underlying changes in functions[30]. We chose a large
131 number of 82 ecosystem variables to cover a range of different ecosystem functions, including
132 above- and belowground plant productivity, nutrient and element cycling, antagonistic and
133 mutualistic multitrophic interactions, and invasion resistance (detailed in Table S1). Variables
134 include measurements of the abiotic environment, plants, and consumers. Information on
135 consumers was separated into different functional groups when possible. Otherwise, different
136 taxonomic groups were separated as these groups indicate not only secondary productivity,
137 but also mediate different ecosystem functions, e.g. herbivory, predation, parasitism,
138 decomposition, scavenging, pollination, and seed predation / dispersal. To ensure that each
139 ecosystem variable was included only once in the analysis, only the measurement in the last
140 available year was selected, thus excluding repeated measures. Correlated ecosystem
141 variables were not excluded *a priori,* as investigating how the relationships among functions
142 affect multifunctionality was an explicit goal of the present study. We also decided against
143 combining different ecosystem variables that appear to be related to the same ecosystem
144 function into a single "true" function, because what is considered an indicator of different
145 functions is arbitrary and depends critically on the research question. For example,
146 aboveground and belowground biomass production of plants are both indicators of overall
147 productivity, yet they are also individual indicators with particular impacts on the ecosystem;
148 aboveground biomass mainly represents carbon fixation, transpiration and potential for light
149 interception, while belowground biomass indicates potential nutrient and water uptake as well
150 as respiration. Similar arguments hold for the different groups of herbivores. While all
151 contribute to overall herbivory, they interact, depending on their feeding guild, with different
152 parts of the food web. In the following, we will refer to 'ecosystem variables that indicate
153 ecosystem functions' as 'functions' for simplicity as is commonly done in studies of
154 multifunctionality[19,20,22,27].

155

156 **Results**

157

158 To quantify the change in overall ecosystem functioning along the experimental gradient of
159 plant species richness, we calculated a multifunctionality index based on all 82 functions.
160 Different indices to quantify multifunctionality have been proposed[18]. Multifunctionality is a
161 multifaceted ecosystem property, much like biodiversity[31], and all of the proposed indices
162 quantify slightly different facets of multifunctionality[18]. We extended the averaging approach
163 proposed for individual functions[18,19,32] to a multivariate approach, based on a principal
164 component analysis (PCA) that analyses the correlation structure among the different
165 functions. The main advantage of this new multivariate index of multifunctionality over the
166 previous approaches[18] is the fact that it accounts for both positive and negative correlations
167 between ecosystem functions, which may otherwise bias results of multifunctionality
168 analyses[33]. We found that many of the functions analysed here were positively or negatively
169 correlated with each other (Fig. S2–4). The overall level of co-linearity was, however, limited,
170 as indicated by the fact that 24 PCA axes were needed to explain 80% of the total variance in
171 functional space (Fig S2–2). A visualisation of the first two principal components showed that
172 the most diverse 60-species plots form a distinct cluster at the right end of the first PCA-axis
173 (Fig. 1-A). Plant species richness was strongly positively correlated with the first principal
174 component axis ($r=0.80$, $t_{79}=12.0$, $p<0.001$). Consequently, plant species richness was the
175 most important single driver of ecosystem functioning in our experiment, because the first
176 principal component represents the maximum variance that can be summarised on one axis.
177 Individual functions that correlated with the first PCA-axis were also positively correlated
178 with plant species richness, e.g., biomass and height of the plant community, bare ground
179 cover (negatively correlated with plant species richness), microbial biomass, and the
180 abundance of earthworms and other animal groups. The PCA-approach was robust against the

181 inclusion of non-normally distributed data on ecosystem functions as demonstrated in a
182 sensitivity analysis using principle coordinates analysis based on Gower-distances (PCoA;
183 Supplementary material S3). Because principal components are uncorrelated, in contrast to
184 the original functions, multifunctionality of a plant community can be related to the scores of
185 the principal components, without adding correlated information. We quantified total
186 functioning of a particular plant community by adding the scores of all PCA-axes, weighted
187 by the eigenvector of the respective axis (see methods). An increase in this multifunctionality
188 index indicates increased functioning because the index was positively correlated with
189 variables characterizing primary (e.g. plant biomass, height, cover, and LAI) and secondary
190 productivity (e.g. number of many belowground fauna groups) as well as soil organic carbon
191 and biomass of microorganisms in the soil (Table S4). The multifunctionality index was
192 negatively correlated with disservices, such as the cover of bare ground and soil bulk density
193 (Table S4).
194
195 The multifunctionality index increased significantly with increasing plant species richness
196 ($F_{1,76}$=8.13, p=0.006; Fig. 1-B). Multifunctionality calculated using previously published,
197 complementary approaches, i.e. the averaging, the threshold and the multiple thresholds
198 approaches[18] confirmed this strong increase in multifunctionality with increasing plant species
199 richness (Fig. S5 A–D). Further, the effect of plant species richness on multifunctionality was
200 robust when restricting the analysis to the 54 ecosystem functions measured in the same year
201 (2004, Table S1; Supplementary material S6). Thus, biodiversity sustains multifunctionality
202 also when the previously demonstrated effects of temporal turnover[12,20] were excluded.
203
204 Next, we analysed how the number of functions used to calculate multifunctionality affected
205 the relationship between biodiversity and multifunctionality, by analysing random subsets of
206 two to 82 ecosystem functions. We observed consistent positive effects of biodiversity on

multifunctionality that, in contrast to simulated results[24], became stronger when a larger number of functions was considered (Fig. 2). Increasingly strong effects of biodiversity on ecosystem multifunctionality with higher numbers of considered functions indicate that in our experiment there are properties of diverse plant communities that were not included in the simulation study[24]. Thus, expected effects of biodiversity on multifunctionality are largest when a high number of ecosystem functions are of interest. However, the strength of the relationship between biodiversity and ecosystem multifunctionality showed large variation around the mean slope for any given number of functions and critically depended on the identity of the ecosystem functions used for calculating multifunctionality. These identity effects imply that studies of multifunctionality based on different functions cannot be directly compared. Identity effects occurred because of trade-offs among ecosystem functions (Fig. S2-1, Table S2-2, Fig. S4-1A) and of functions that were only weakly or even negatively related to multifunctionality (Fig. S4-1B, Table S4). Likely including such functions or functions that are well sustained by low biodiversity in the random draw, explains the slight decrease in average multifunctionality when very high numbers of ecosystem functions were considered (Fig. 2). For particular subsets of functions, biodiversity had only minor effects on ecosystem multifunctionality (Fig. 2). This can explain why studies may also find weak effects of biodiversity on ecosystem multifunctionality[18].

Increasingly strong effects of biodiversity on multifunctionality when more functions are considered were also confirmed when we calculated the proportion of plant species that contributed to functioning using the 'turnover' approach[17]. For each ecosystem function, informative species effects were extracted from a full model including the presence-absence data of all 60 plant species as explanatory variables, using a stepwise AIC-approach. For each number of ecosystem functions between 1 to 82, up to 2000 random subsets of functions were drawn, and the proportion of species (out of the total of 60) that had informative, positive

effects on at least one of the functions in the subset was calculated. In the same way, negative effects were analysed in a separate analysis. The proportion of species that contributed positively to functioning increased strongly with the number of functions considered (Fig. 3). Using a critical ΔAIC value of 2, as proposed by Hector and Bagchi [17] in the original description of the turnover approach, the proportion of species contributing to functioning was not statistically different from one, i.e., all species contributed to functioning when ten or more functions were analysed (see also Fig. S7-1A). These results exceed the proportions of species that were shown to contribute to functioning in earlier studies[17,20] also when only ecosystem functions measured in the same year (2004, Table S1) were used in a sensitivity analysis (Fig. S6-1A). In addition to positive effects of the presence of species on functioning, every species also decreased at least one of the ecosystem functions investigated (Fig. S7-1B). Yet, functioning increased with higher diversity because effect-sizes of positive contributions were higher than of negative contributions (Fig. S7-2). We calculated a null model based on data where the presence of species in plots had been permutated over the plots to disrupt the association between the presence of species and ecosystem functioning (see methods). Comparison to the null model showed that, when using a critical ΔAIC value of 2, a high number of false positive species effects inflate the proportion of species with informative effects. This inflation of the number of informative effects was confirmed in a simulation study (Supplementary material S8). To compensate for the statistical effect of fitting a large number of models estimating many parameters, we recalculated the analysis with a series of increasingly strict critical ΔAIC values that needed to be surpassed for the effect of the presence of a species to be considered informative (see methods). Using increasingly stricter ΔAIC values, the proportion of species with informative effects continuously declined; as was to be expected (Fig. 3A-F; supplementary material S8). The proportion of species showing effects for the permutated data declined faster than for the measured data so that the asymptote for the proportion of species with effects was about 20 percent points higher for the

measured data than for the permutated data (Fig. 3D-F). Thus, about 20% of the plants in the species pool showed effects on ecosystem functioning that could be unambiguously separated from potential statistical artefacts and are thus informative beyond doubt. It is important to notice that this number is an extremely conservative estimate because a) the turnover approach does not account for interactions between species (complementarity), and b) with such strict criteria the chances of rejecting true effects increases. The proportion stated here cannot be compared to previously published estimates of the proportion of species pool affecting functioning[17,20] as these studies used much less strict criteria for the detection of effects. Given that in the design of the experiment every species occurs only in a minor fraction of the plots and given the proportion of species with effects increased with the number of functions considered and that the number of functions in real-world ecosystems likely exceeds even the 82 ecosystem functions considered in this study, we conclude that the proportion of species individually contributing to ecosystem functioning is likely much higher than can be shown here.

## Discussion

Our findings have two major implications for the management of ecosystems. First, our results demonstrate that not all ecosystem services can be maximised simultaneously when these services rely on functions that show trade-offs[34,35]. Thus, management to maximise a particular ecosystem service will probably decrease provisioning of other ecosystem services[36] and may not maximise but may even decrease multifunctionality. A similar result was found with respect to the effect of land use on the provisioning of 'ecosystem service bundles', where the magnitude and even the direction of effects depended on the composition and weighting of ecosystem services in a bundle[37]. However, our analysis also indicates a) that adding species (if it is still possible to add a species) should be beneficial as adding a species to an ecosystem would likely increase some ecosystem function (more than it would

decrease others), and b) that it is possible to maximise particular functions, such as biomass production, and simultaneously favour other functions such as increased water- or nutrient-use efficiency, resulting in reduced environmental impacts combined with potential economic benefits. Second, our results increase misgivings about the assumption that managing ecosystems to maximise ecosystem service provisioning guarantees the preservation of biodiversity, as would be expected if high biodiversity always underlies high ecosystem service provisioning[38]. While biodiversity was the strongest driver of ecosystem functioning in our study underlining its importance, our results show that the particular combination of ecosystem functions considered determines whether and to which extent multifunctionality is related to biodiversity (Fig. 2). Consequently, managing an ecosystem to maximise biodiversity will not necessarily maximise a particular subset of functions for which managers are aiming, and management for services will not necessarily protect biodiversity. We thus emphasise that ecosystem service provisioning cannot replace high biodiversity as the aim of management interventions. The need for specific management to protect biodiversity is further underlined by the result that only a minor fraction of the species pool showed a significant functional importance of the individual species.

## References


1 Millennium Ecosystem Assessment. *Millennium Ecosystem Assessment - Ecosystems and Human Well-being: Biodiversity Synthesis*. (World Resources Institute, 2005).

2 Butchart, S. *et al.* Global biodiversity: indicators of recent declines. *Science* **328**, 1164 - 1168, (2010).

3 Maxwell, S., Fuller, R., Brooks, T. & Watson, J. Biodiversity: The ravages of guns, nets and bulldozers. *Nature* **536**, 143, (2016).

4 Hooper, D. U. *et al.* Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.* **75**, 3-35, (2005).

5 Hector, A. *et al.* Plant diversity and productivity experiments in European grasslands. *Science* **286**, 1123-1127, (1999).

6 Tilman, D., Wedin, D. & Knops, J. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* **379**, 718-720, (1996).

7 Johnson, K. H., Vogt, K. A., Clark, H. J., Schmitz, O. J. & Vogt, D. J. Biodiversity and the productivity and stability of ecosystems. *Trends Ecol. Evol.* **11**, 372-377, (1996).

8 Naeem, S. Ecosystem consequences of biodiversity loss: The evolution of a paradigm. *Ecology* **83**, 1537-1552, (2002).

9 Loreau, M. Biodiversity and ecosystem functioning: A mechanistic model. *Proc. Natl. Acad. Sci. USA* **95**, 5632-5636, (1998).

10 Fetzer, I. *et al.* The extent of functional redundancy changes as species' roles shift in different environments. *Proc. Natl. Acad. Sci. USA* **112**, 14888-14893, (2015).

11 Walker, B. H. Biodiversity and Ecological Redundancy. *Conserv. Biol.* **6**, 18-23, (1992).

12 Allan, E. *et al.* More diverse plant communities have higher functioning over time due to turnover in complementary dominant species. *Proc. Natl. Acad. Sci. USA* **108**, 17034-17039, (2011).

13 Schwartz, M. W. *et al.* Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia* **122**, 297-305, (2000).

14 Srivastava, D. S. & Vellend, M. Biodiversity-ecosystem function research: Is it relevant to conservation? *Annual Review of Ecology Evolution and Systematics* **36**, 267-294, (2005).

15 Sanderson, M. *et al.* Plant species diversity and management of temperate forage and grazing land ecosystems. *Crop Sci.* **44**, 1132-1144, (2004).

16 Zavaleta, E. S., Pasari, J. R., Hulvey, K. B. & Tilman, G. D. Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity. *Proc. Natl. Acad. Sci. USA* **107**, 1443-1446, (2010).

17 Hector, A. & Bagchi, R. Biodiversity and ecosystem multifunctionality. *Nature* **448**, 188-190, (2007).

18 Byrnes, J. E. K. *et al.* Investigating the relationship between biodiversity and ecosystem multifunctionality: challenges and solutions. *Meth. Ecol. Evol.* **5**, 111-124, (2014).

19 Maestre, F. T. *et al.* Plant species richness and ecosystem multifunctionality in global drylands. *Science* **335**, 214-218, (2012).

20 Isbell, F. *et al.* High plant diversity is needed to maintain ecosystem services. *Nature* **477**, 199-202, (2011).

21 Hillebrand, H. & Matthiessen, B. Biodiversity in a complex world: consolidation and progress in functional biodiversity research. *Ecol. Lett.* **12**, 1405-1419, (2009).

22 Lefcheck, J. S. *et al.* Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. *Nat. Commun.* **6**, (2015).

23 Soliveres, S. *et al.* Locally rare species influence grassland ecosystem multifunctionality. *Phil. Trans. R. Soc. B* **371**, 20150269, (2016).

24 Gamfeldt, L. & Roger, F. Revisiting the biodiversity–ecosystem multifunctionality relationship. **1**, 0168, (2017).

25 Allan, E. *et al.* A comparison of the strength of biodiversity effects across multiple functions. *Oecologia* **173**, 223-237, (2013).

26 Roscher, C. *et al.* The role of biodiversity for element cycling and trophic interactions: an experimental approach in a grassland community. *Basic Appl. Ecol.* **5**, 107-121, (2004).

27 Bowker, M. A., Maestre, F. T. & Mau, R. L. Diversity and patch-size distributions of biological soil crusts regulate dryland ecosystem multifunctionality. *Ecosystems* **16**, 923-933, (2013).

28 Reiss, J., Bridle, J. R., Montoya, J. M. & Woodward, G. Emerging horizons in biodiversity and ecosystem functioning research. *Trends Ecol. Evol.* **24**, 505-514, (2009).

29 Jax, K. *Ecosystem functioning*. (Cambridge University Press, 2010).

30 Meyer, S. T., Koch, C. & Weisser, W. W. Towards a standardized Rapid Ecosystem Function Assessment (REFA). *Trends in Ecology and Evolution* **30**, 390-397, (2015).

31 Purvis, A. & Hector, A. Getting the measure of biodiversity. *Nature* **405**, 212-219, (2000).

32 Hooper, D. U. & Vitousek, P. M. Effects of plant composition and diversity on nutrient cycling. *Ecol. Monogr.* **68**, 121-149, (1998).

33 Dooley, Á. *et al.* Testing the effects of diversity on ecosystem multifunctionality using a multivariate model. *Ecol. Lett.*, (2015).

34 Lovell, S. T. & Johnston, D. M. Creating multifunctional landscapes: how can the field of ecology inform the design of the landscape? *Front. Ecol. Environ.* **7**, 212-220, (2009).

35 Foley, J. A. *et al.* Global consequences of land use. *Science* **309**, 570-574, (2005).

36 Bullock, J. M., Aronson, J., Newton, A. C., Pywell, R. F. & Rey-Benayas, J. M. Restoration of ecosystem services and biodiversity: conflicts and opportunities. *Trends Ecol. Evol.* **26**, 541-549, (2011).

37 Allan, E. *et al.* Land use intensification alters ecosystem multifunctionality via loss of biodiversity and changes to functional composition. *Ecol. Lett.* **18**, 834-843, (2015).

38 Reyers, B., Polasky, S., Tallis, H., Mooney, H. A. & Larigauderie, A. Finding common ground for biodiversity and ecosystem services. *Bioscience* **62**, 503-507, (2012).

**Acknowledgements**

We thank E. Marquard, Ilone Kertscher, Y. Kreutziger, S. Rosenkranz, and A. Sabais for providing additional data and Thomas Lewinsohn for comments on the manuscript. We thank the gardeners, technicians, student helpers and managers of the Jena Experiment for their work. The Deutsche Forschungsgemeinschaft (FOR 456 and FOR 1451), as well as the Swiss National Science Foundation, financed the Jena Experiment.

388

389 **Author Contributions**

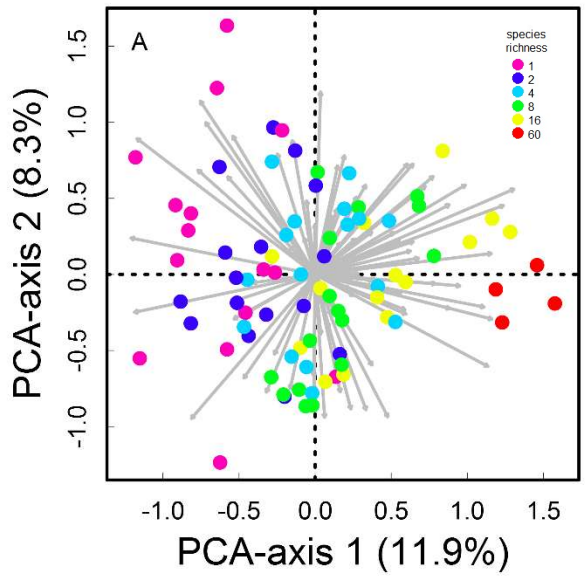
390 S.T.M, R.P, H.H. , and W.W.W conceived the study and developed the analytical procedure;
391 S.T.M. and R.P performed the analyses with contributions by W.F.; all authors contributed
392 measured data; S.T.M and W.W.W. wrote the paper with contributions from all authors to
393 writing and editing of the paper.

394

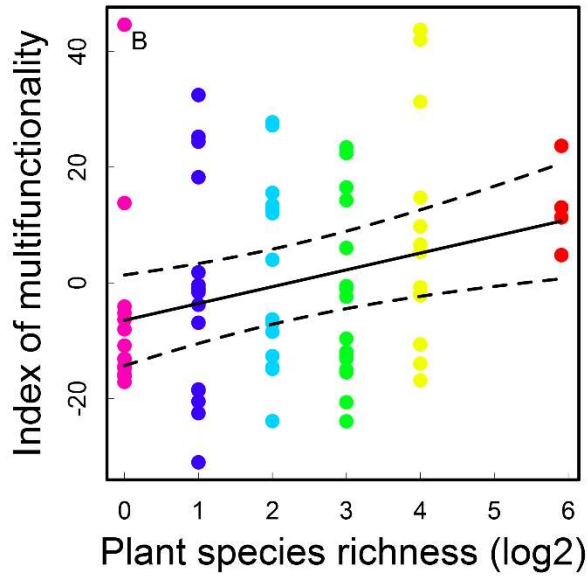
395

396 **Figure 1:** Effects of biodiversity on multifunctionality. (A) The graph shows the position of
397 each plot (coloured dots) in a multifunctional space spanned by the first two axes derived
398 from a principal component analysis (PCA) based on 82 different ecosystem functions
399 measured in the Jena Experiment. The red dots (60-species mixtures) form a distinct cluster at
400 the right-hand side of the graph far from the centre of the plot. Each of the functions is shown
401 as a grey arrow (vector) pointing in which direction of the ordination space it increases in
402 value. The angles between function vectors represent the degree of correlation between them.
403 As angles between function vectors in the PC1/PC2 ordination plane can be distorted by
404 relationships with higher PCA axes, precise correlation coefficients among all functions are
405 given in Fig. S2-4 (supplementary material). Graphs with labelled arrows for the functions
406 can be found in Fig. S2-1. (B) Effect of plant species richness on ecosystem
407 multifunctionality as found in the Jena Experiment. The multifunctionality index was
408 calculated by summing up the PCA-axis scores for all experimental plots weighted by the
409 eigenvalue of the respective PCA-axis. The solid black line represents the effect of a linear
410 model fit, the dashed lines the 95% confidence intervals around the fit.

411


A
species richness
1
2
4
8
16
60
PCA-axis 2 (8.3%)
PCA-axis 1 (11.9%)
-1.0
-0.5
0.0
0.5
1.0
1.5

412


B
Index of multifunctionality
Plant species richness (log2)
-20
0
20
40
0
1
2
3
4
5
6

413

**Figure 2:** Effects of number and identity of ecosystem functions on the relationship between plant species richness and multifunctionality. Each open circle shows the slope between the multifunctionality index and plant species richness, for a particular random subset of the 82 ecosystem functions included in the analysis. Red filled circles show the mean slope for a particular number of functions, resulting from up to 500 random draws of this particular number of ecosystem functions.

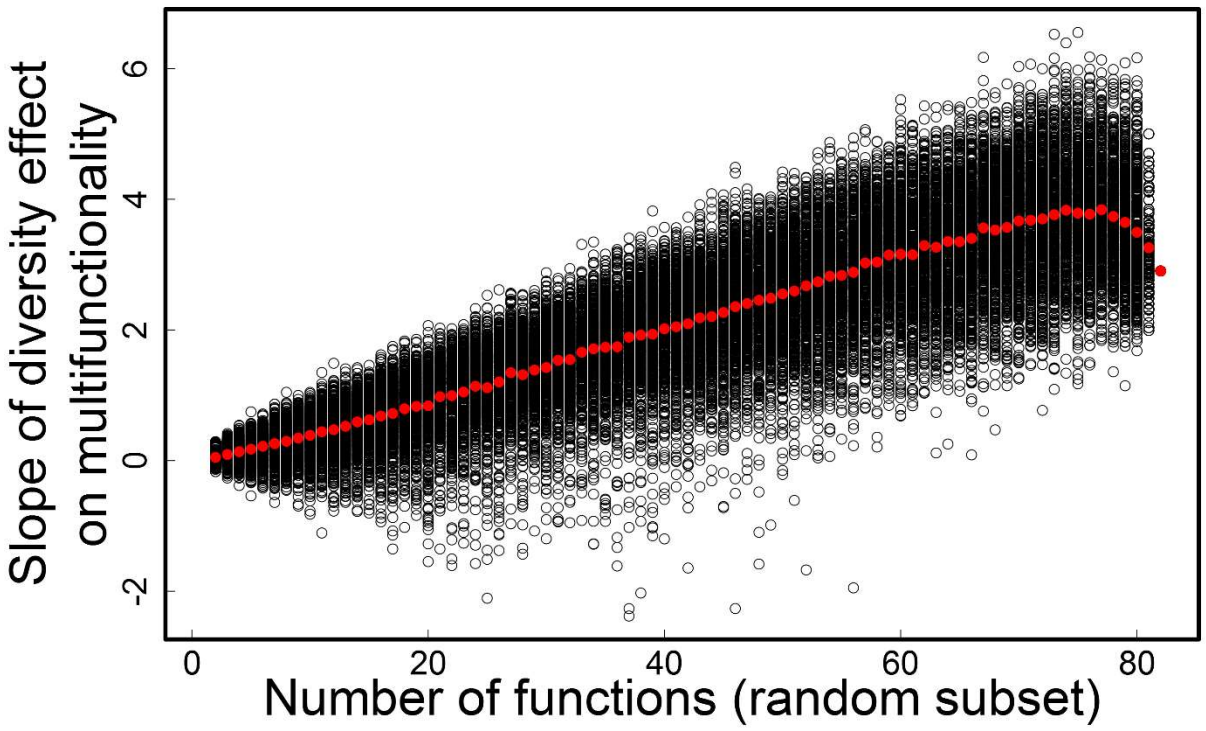
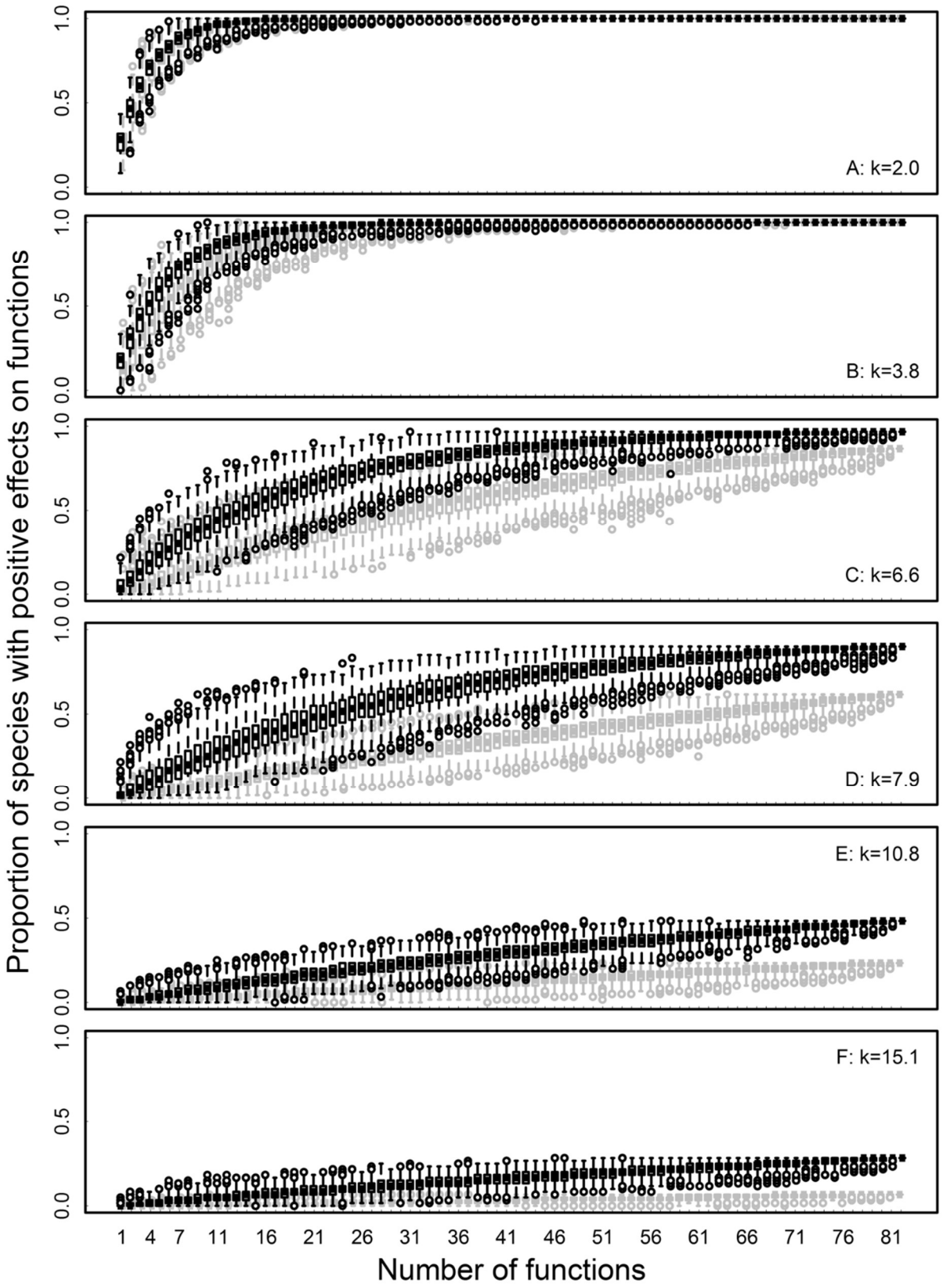


**Figure 3:** Proportion of the plant species pool that contributes positively to functioning when an increasing number of ecosystem functions is analysed simultaneously. The plant species pool contains 60 species, and the total number of functions considered was 82. Shown are the average proportion together with quartiles, the 1.5 times interquartile range as whiskers, and outliers beyond this range as dots; all calculated for up to 2000 random draws of each number of functions from the total of 82. Grey boxes show results of a null-model for which the measurements of each function have been permutated over the plots of the experiment to disrupt associations between the presence of species and the level of functioning in a plot (see details in the methods). Each panel gives the results of an analysis with an increasingly strict criterion for the effect of a species to be considered informative. The k-values stated are the minimum ΔAIC-value needed for the comparison of a model containing the presence of a species as explanatory variable compared to a simpler model without it to be considered informative.


Proportion of species with positive effects on functions
A: k=2.0
B: k=3.8
C: k=6.6
D: k=7.9
E: k=10.8
F: k=15.1
0.0
0.5
1.0
1 4 7 11 16 21 26 31 36 41 46 51 56 61 66 71 76 81
Number of functions

436

437

438